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Diverse nature of ubiquitous microborings in Cenomanian corals (Saxonian Cretaceous Basin, Germany)

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ABSTRACT

Upper Cenomanian rocky shore conglomerates exposed in the abandoned Ratssteinbruch quarry in Dresden (Saxonian Cretaceous Basin, Eastern Germany) contain numerous small coral colonies. The skeletons are commonly encrusted with thin ferruginous microbial crusts. Skeletal elements, especially radial elements (septa), contain abundant microborings filled with iron oxyhydroxides. Natural casts of microborings were studied under SEM. Two categories of microborings (2–12 μm in diameter) were distinguished in respect of their time of production. Type 1 microborings occur in the inner part of the colonies and are typically distributed more or less along the septa in the direction of the coral growth. This type is represented by *Ichnoreticulina elegans* (most common traces; produced by chlorophyte green alga), *Scolecia filosa* (traces of cyanobacteria), and much more rarely by *Conchocelichnus seilacheri* (traces of red algae). They were produced during coral life (*in vivo*), and provide insight into the very poorly recognised skeleton microbiome of fossil corals. Chlorophyte alga *Ostreobium quekettii* – the most common microendolith in the skeletons of living modern corals – produces *I. elegans*, which dominates the Type 1 microborings. Type 2 microborings include *I. elegans*, *S. filosa*, *Scolecia serrata* (made by bacteria) and undetermined microborings. They occur directly below the microbial crusts coating the entire colony, or below thin ferruginous films coating the surfaces of skeletal elements. Microborings are distributed randomly or are more or less perpendicular to skeleton surfaces, demonstrating that Type 2 microborings were evidently made by microendoliths after coral death (post-mortem), when skeletal elements were exposed.

1. Introduction

Microborings are the penetration traces in hard substrates produced by microorganisms (microendoliths, or more precisely microeuendoliths; Golubic et al., 1981) which represent mainly algae, bacteria and fungi. They are common in recent and fossil carbonate and non-carbonate rock components. Microborings produced post-mortem are a useful tool for interpreting sedimentary environment parameters (Golubic et al., 1975; Vogel et al., 2000; Cockell and Herrera, 2008; Tribollet et al., 2011; Wisshak, 2012). However, much less is known about the boring microorganisms that inhabited skeletons during an organisms' life. Boring microorganisms are ubiquitous in modern living corals, constituting the coral skeleton microbiome. They are much more important for the coral host and reef functioning than previously assumed (e.g., Fine and Loya, 2002; Ainsworth et al., 2017; Ricci et al., 2019; Pernice et al., 2020). The fossil record of microborings produced *in vivo* in coral skeletons is very sparse (Elias and Lee, 1993; Kołodziej et al., 2012, 2016; Salamon, 2017; Salamon et al., 2019).

Empty microborings allow the preparation of resin casts that can be studied under the scanning electron microscope (SEM) to determine the ichnotaxa, and thus also what produced the traces. Microborings in fossil carbonate substrates are commonly filled with calcite, which means that detailed studies of microborings are practically impossible. If microborings are filled with non-carbonate minerals, then the dissolution of the $CaCO_3$ forming the skeleton allows three-dimensional natural casts to be obtain (e.g., Golubic et al., 1975; Schnick, 2017).

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Such fossilisation is common in corals from the upper Cenomanian conglomerate outcropping in the Ratssteinbruch quarry in Dresden (Figs. 1–2), enabling microborings ichnotaxonomy to be studied. Corals in these conglomerates are common (Löser, 1989, 2014). Gradziński et al. (1996) described ferruginous microbialite crusts on coral skeletons and recognised microborings filled with iron-rich minerals, but the first data on the ichnotaxonomy of these traces was provided by Salamon (2017) and Salamon et al. (2018). In this paper we document the most common microborings. Their distribution pattern allows us to distinguish two diverse ecological groups of microendoliths producing these traces.

2. Geological setting

2.1. Geological background

Coral-bearing basal conglomerate in the Ratssteinbruch in SW Dresden (Dresden-Dölzschen) (Fig. 1C) belongs to the upper Cenomanian Dölzschen Formation of the Elbtal Group (lower Cenomanian to middle Coniacian) deposited in the Saxonian Cretaceous Basin (Figs. 2–3). This sedimentary sequence was formed in a strait between the Mid-European Island in the southwest and the West-Sudetic Island in the northeast (see fig. 1B in Wilmsen et al., 2019). During the early Late Cretaceous this sedimentary basin was situated in an intermediate position between the temperate Boreal Realm in the north and the Tethyan warm water areas in the south. Lithologically, the Elbtal Group encompasses shallow marine conglomerate, slightly deeper marine sandstone, calcareous siltstone, marly limestone and marl. Coral-bearing deposits in the area of Meißen (Meißen Formation) are results of the early middle Cenomanian transgression, the first major early Late Cretaceous transgression in Saxony. Macrofossils coated by ferruginous microbial crusts occur there as well, but are not considered in this paper. There were two successive transgressive pulses in the late Cenomanian, culminating in the earliest Turonian maximum flooding event (Niebuhr et al., 2020). The Dölzschen Formation at the Ratssteinbruch quarry was believed for a long time to belong to a Cenomanian–Turonian transition zone. These deposits are now dated entirely as late Cenomanian and corresponds to the *Metoicoceras geslinianum* and *Neocardioceras juddii* zones (Fig. 3). The coral-bearing basal conglomerate belongs to the *geslinianum* Zone only (Wilmsen and Nagm, 2013). Niebuhr and Wilmsen (2014, 2016) provided details about the geology of the study area and the fossil fauna.

Approximately five metres of the Cenomanian deposits lay on the Upper Carboniferous monzonite crystalline basement (exploited until the 1960s). The strata are slightly inclined (5°) to the northeast. The coral-bearing conglomerate consists of large, well-rounded monzonite boulders and pebbles in a hard grey limestone containing abundant glauconite. Conglomerate thickness varies up to one meter. In pockets in the crystalline basement the conglomerate is locally thicker (Tröger, 1956). The size of pebbles decreases in the upper part of conglomerate layer, and layers of limestone change to marls and sandy limestone. The up-section following deposits indicate an increase in water depth, and only silty-sandy (marly) limestones were sedimented (so called "Pläner" from "Plauener Stein").

Macrofossils are abundant in the conglomerate; they are represented by corals, gastropods, bivalves, brachiopods, and, less abundant, belemnites, shark teeth, bryozoans, sponges, and serpulids. The fauna indicates a very shallow marine environment. The organisms are not found in life position, but the corals were

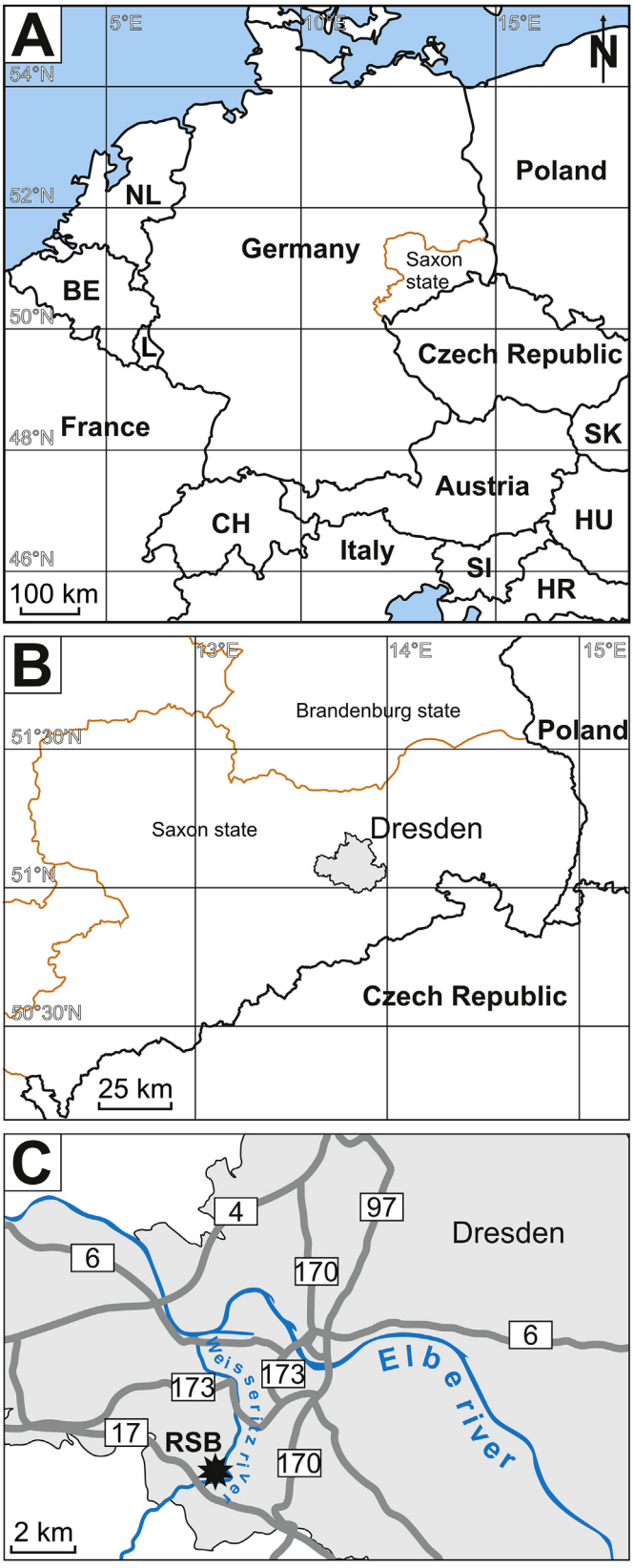

Fig. 1. Geographic position of Saxony (**A**), Dresden (**B**) and location of the Ratssteinbruch quarry (RSB and asterisk) (**C**).

Fig. 2. General geological map of the Dresden area (based on Wilmsen et al., 2019). The Ratssteinbruch quarry is marked with the asterisk.

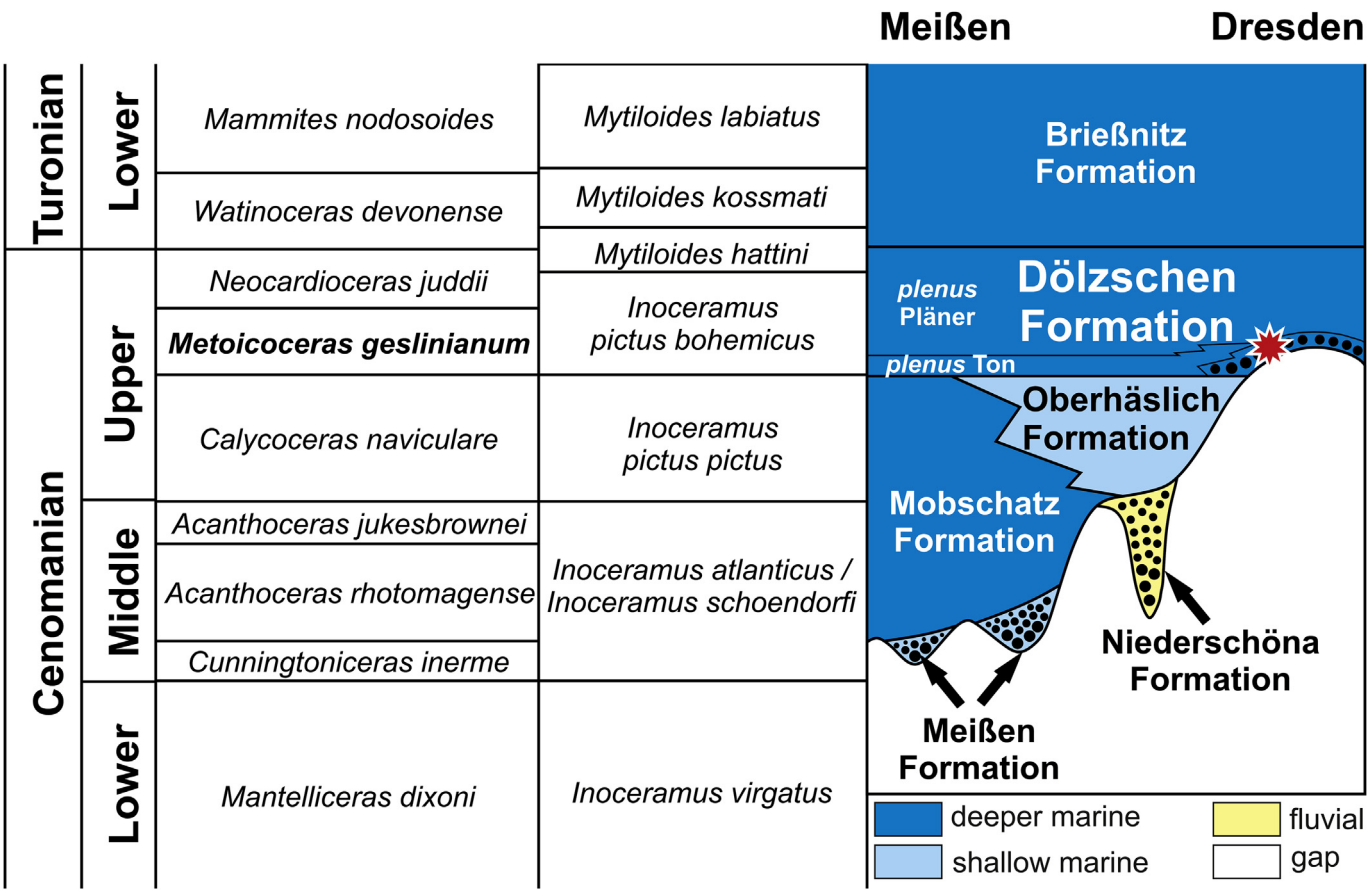

Fig. 3. Litho- and biostratigrapahy of the Cenomanian–lower Turonian of Meißen and Dresden area (lower Elbtal Group) based on Wilmsen et al. (2019). Asterisk indicates the upper Cenomanian coral-bearing conglomerates of the Dölzschen Formation in the Ratssteinbruch quarry (*Metoicoceras geslinianum* Zone).

probably not transported far away. The corals partially suggest a position in the matrix according to their centre of gravity, so the large cup-like colonies of *Vallimeandra fromenteli* (Bölsche) (Löser, 1989) are always found in a upside down position. The fossils are in various states of preservation; sometimes they are rounded and broken, sometimes very well preserved.

Hanns Bruno Geinitz wrote between 1871 and 1875 the first papers on the fossils from the Upper Cretaceous of Saxony (see Niebuhr, 2014). Tröger (1956) provided extensive lists of the fauna of the Ratssteinbruch area. The most recent and most comprehensive compilation of fossils from the area can be found in Niebuhr and Wilmsen (2014, 2016).

2.2. Corals from the Ratssteinbruch quarry

Corals are the most abundant fossils in the upper Cenomanian conglomerate of the Ratssteinbruch area, both colonial and solitary forms (Löser, 1989, 2014). The colonies rarely reach more than 5 cm in diameter, but there are some large colonies with a diameter of up to 35 cm. The taxonomy is highly diverse. Nearly 60 coral species where reported in Löser (2014) for the whole Upper Cretaceous (Cenomanian–Turonian) of Saxony, distributed among eleven Scleractinian superfamilies and one octocorallian family. Thirty-five species were reported from the Ratssteinbruch area, from the following families: Actinastraeidae, Agatheliidae, Helioporidae, Latomeandridae, Negoporitidae, Phyllosmiliidae, Solenocoeniidae, Thamnasteriidae, and the informal *Diplocoenia* and *Plesiosmilia* groups.

3. Material and methods

The samples studied are from the Rattsteinbruch, a former monzonite quarry that lies in the valley of the small Weisseritz River on the southwest margin of the city of Dresden (Fig. 1B-C). It is subdivided into northern and southern areas. The fossil-bearing deposits are only accessible in the southern area, and all material studied here is from this section.

The samples were mostly collected by H. Löser in 1981–1995. Most samples and thin sections are housed at the Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Dresden, Germany, under the signature SaKL, and some are at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany, under the signature 2009 XVII. Additionally, one hundred and sixteen thin sections were also made and housed at the Institute of Geological Sciences, Jagiellonian University in Kraków (K. Salamon's collection under the signature Drezno from R1 to R115). Thin sections were examined and preselected under the petrographic microscope (plain light) according to the presence of microborings. Thirty-nine etched thin sections and four small samples etched in diluted hydrochloric acid (3–3.5%) were observed under the Hitachi S-4700 scanning electron microscope (SEM) at the Jagiellonian University.

4. Results

4.1. Coral-associated deposit and ferruginous crusts

The carbonate matrix (within conglomerate), including a few millimetres layer attached to the external part of coral skeletons, and deposit within small intraskeletal voids, is a bioclastic packstone with glauconite and quartz grains (Figs. 4–5).

All colonies and solitary corals, like many other macrofossils, are encrusted by thin, brownish ferruginous crusts, usually up to a few millimetres thick (Figs. 4B, 5, 6, 10A, C), while skeletal elements, especially radial elements (septa), are coated with very thin ferruginous films (usually 2–20 μm thick; Fig. 7). The crusts are commonly opaque under the petrographic microscope (Figs. 5A, 9), rarely laminated (Figs. 4B, 6B), but the SEM images of etched samples reveal lamination (Figs. 5B, 10A–C). Rare filaments within crusts occur only in small embedded clasts (Fig. 9A). The interseptal

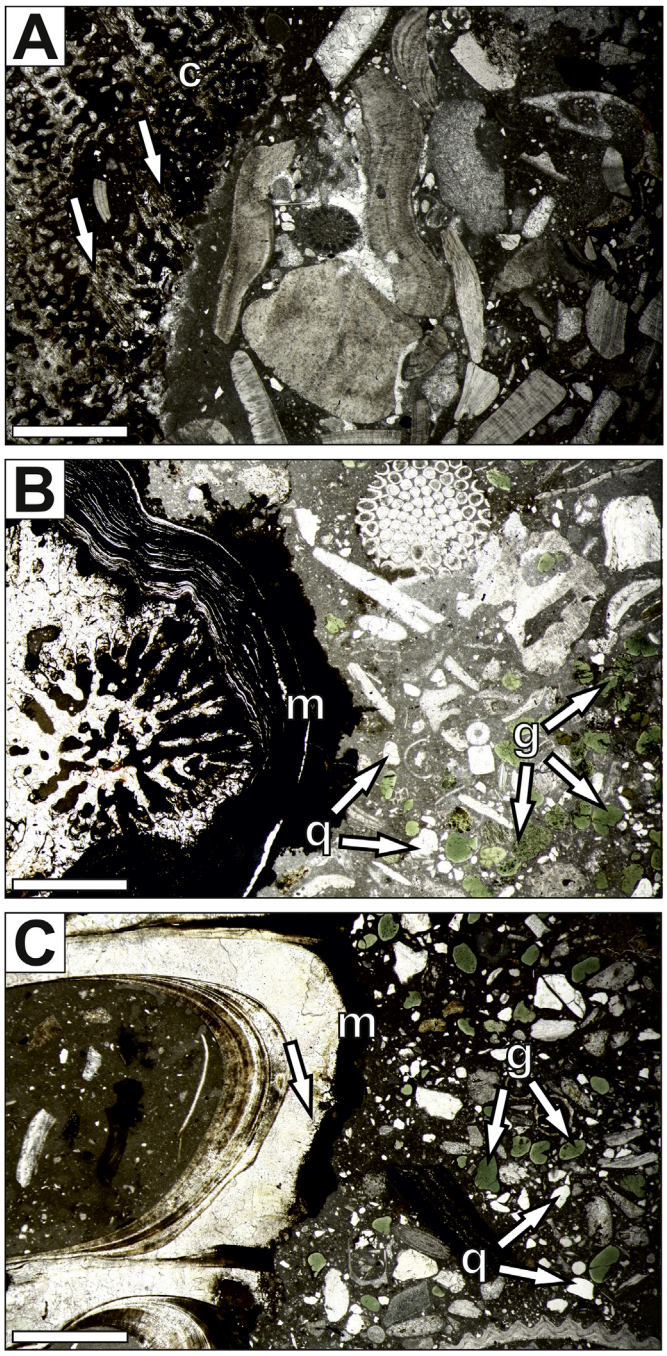

Fig. 4. Microfacies of carbonate sediment surrounding the studied coral colonies: bioclastic packstone with glauconite (g) and quartz (q) under the petrographic microscopes (plain light). **A.** Longitudinal section through the coral colony (c). The interseptal space is filled with ferruginous deposit. Numerous microborings are locally visible in septa (arrows). Small bioclasts (mostly fragments of bivalves) are devoid of ferruginous crusts and contain only rare microborings not filled by iron-rich minerals. **B.** Coral colony coated by ferruginous, laminated microbial crust (m). The interseptal space at outer part of the corallite filled with ferruginous sediment. **C.** Fragment of a gastropod shell coated by ferruginous crust (m). Common microborings occur only directly below the crust (arrow), and are rare in the inner part of the shell. Scale bars = 5 mm.

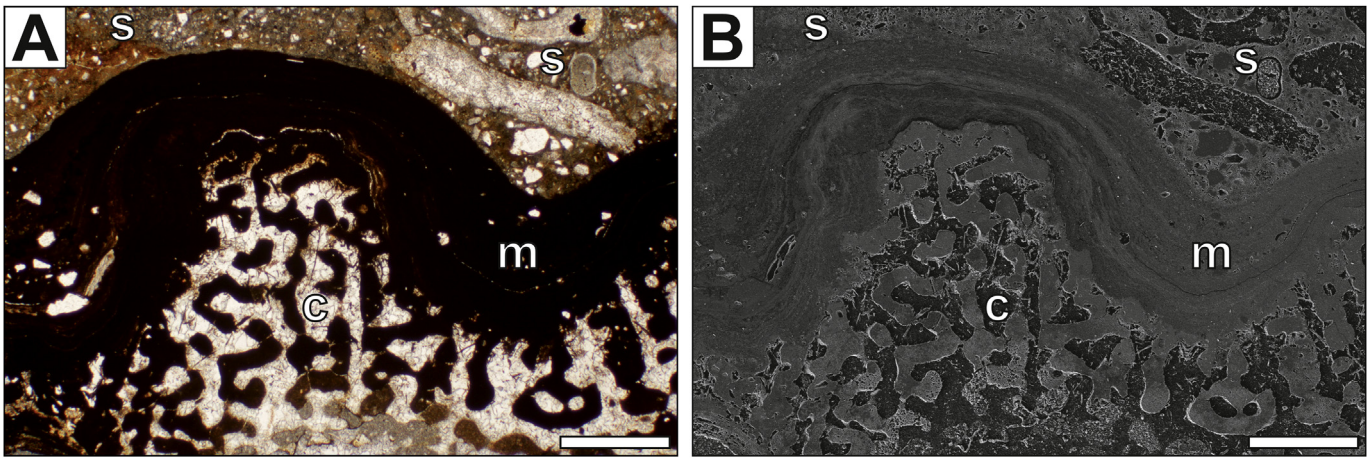

Fig. 5. Ferruginous microbial crust (m) around the coral colony (c) in a longitudinal section under the petrographic (A) and SEM microscopes (B). **A.** Opaque microbial crust on a coral skeleton and surrounded by a carbonate sediment (s). **B**. The same area, but the sample was etched. The internal lamination of the crust is clearly visible. Scale bars = 500 μm.

spaces are filled wholly or partly with ferruginous sediment (Figs. 4A–B, 5A, 6A, 7A, 8, 9, 10). Common microborings occur also in other macrofossils coated by ferruginous crusts (Fig. 4C), but they are absent or rare in small bioclasts without such crusts (Fig. 4A–B).

4.2. Microborings

Microborings are abundant in coral skeletons. The term 'microborings' is used in this paper, even though microborings are filled with iron oxyhydroxides, and it was in fact the natural casts of microborings (galleries) that were examined in this study. SEM studies revealed their distribution pattern within skeletal elements and allowed ichnotaxa to be distinguished.

Two microboring types are distinguished on the basis of their relationship to the surface of coral colonies and skeletal elements (septa, wall, columella) (Figs. 6B, 10D for generalised view). These microborings are mostly 2–4 μm in diameter (except 12 μm thick microborings in Type 2). They are generally straight to slightly curved, and branched or unbranched.

Type 1 (Figs. 6B, 7, 8, 10D). This type occur in the entire coral colony, including up to the inner few centimetres below the colony surface, but the detection of microborings is closely related to the range of ferruginous fillings. In some cases microborings are detectable less than 1 mm below the surface, because more inner part of coral skeleton was not affected by ferruginization. The galleries are clearly concentrated in the central parts of the septa and other skeletal elements, oriented more or less upward, in the direction of the coral growth (Figs. 6B, 7A–B, 8, 10D). In transverse section dominantly upward-oriented microborings are marked as numerous dotes (Fig. 7C–D). The following ichnospecies were identified: *Ichnoreticulina elegans* (Radtke, 1991) (most common; approx. 3–5 μm in diameter; Figs. 7A–B, 8A–B), *Scolecia filosa* Radtke, 1991 (approx. 2 μm), and the much rarer *Conchocelichnus seilacheri* Radtke, Campbell & Golubic, 2016 (galleries approx. 10 μm in diameter; Fig. 8C–D). *I. elegans* microborings bifurcate rarely, but usually in the same direction as the top surface of the colony (Figs. 7B, 8B).

Type 2 (Figs. 6B, 9, 10). Microborings occur directly below the ferruginous crusts coating the external surface of coral colonies (Fig. 10B–C) or below thin ferruginous films on skeletal elements (mostly septa; Figs. 9, 10D–E) as well as below the surface of borings made by macroorganisms. Natural casts of microboring tunnels are mainly randomly oriented (Figs. 9, 10B) or more or less parallel to the surface (Fig. 10D–E). In rare examples, galleries are directed downwards, perpendicular to the surface of the colony (Fig. 10C). Spots of dense, thick galleries in dense networks with difficult to determine general patterns are also commonly present, especially in transverse section (Figs. 9C, 10A–B). In most cases only short fragments of galleries in dense networks are found, which means that ichnospecies are hard to identify; however, some 60% of microborings have been taxonomically determined: *I. elegans* (Fig. 10B, E), *S. filosa* (Fig. 10C, E) (of similar diameters as in Type 1), *Scolecia serrata* Radtke, 1991 (approx. 2 μm; Fig. 10B). Undetermined microborings include relatively thick microborings (approx. 12 μm in diameter; Fig. 10B) and extremely rare isolated shack-shape swellings. Networks of microborings which occur below thick encrustations on almost the entire outer surface of coral colonies can reach up to 250 μm in depth (Figs. 9A, 10C). These occurring in the external part of skeletal elements (mostly septa) are much shorter, up to 100 μm (Fig. 10D–E).

Common microborings occur also in other macrofossils coated with ferruginous crusts. They have not been studied in detail, but preliminary observations of bivalve and gastropod shells, revealed that microborings mostly occur directly below ferruginous crusts (Fig. 4C), and are rare in the more inner part of shells, even though the thickness of these shells is much smaller than the diameter of coral colonies. Microborings are absent or very rare in small bioclasts that are not coated by such crusts (Fig. 4A–B).

5. Discussion

5.1. Ferrugenization

The presence of ferruginous crusts and iron-filled microborings in corals and other large fossils on the one hand, and the absence or the rarity of ferruginous crusts and microborings in other fossils, on the other hand, indicate that the fossils in the conglomerate studied derived from different parts of the shallow-water environment, showing different taphonomic histories of skeletal elements. Gradziński et al. (1996) preliminary described ferruginous crusts on corals (mostly), bivalves and gastropods from Ratssteinbruch. In their interpretation, the iron, microbially bound as iron oxyhydroxides, probably derived from the nearby weathered monzonite basement rocks. Microborings are common in modern biotic and abiotic carbonate substrates in shallow-water environments, but are poorly or not preserved in fossil samples. Ferrugenization, possibly more intensive close to the source of iron, certainly

favoured the preservation of microborings in the corals studied (and in macrofossils), despite skeleton diagenesis.

5.2. *Type 1 microborings: traces produced* in vivo

Type 1 microborings were produced from the inside of the skeleton outward, as shown by Le Campion-Alsumard et al. (1995) in a classic case study of microendoliths in live modern corals. Microborings are typically distributed along the septa in the direction of the coral growth, because the boring phototrophic microorganisms had to keep up with the coral's skeleton accretion. These microborings unlike those of Type 2, are not post-mortem, but were produced *in vivo* by coral-associated (symbiotic in a broad meaning) microendoliths.

Most common traces are *Ichnoreticulina elegans* produced by the chlorophyte green alga *Ostreobium quekettii* Bornet & Flahault, 1889 (Radtke, 1991). Others were produced by the cyanobacterium *Plectonema terebrans* Bornet & Flahault ex Gomont, 1892 (producer of ichnospecies *Scolecia filosa*), while ichnospecies *Conchocelichnus seilacheri* is produced by several genera of bangialean red algae (Radtke et al., 2016).

Boring microorganisms (algae, cyanobacteria, fungi) *in vivo* associated with corals are commonly reported from the skeletons of modern species (e.g., Lukas 1974; Le Campion-Alsumard et al., 1995; Golubic et al., 2005; Tribollet, 2008). They belong to the coral skeleton microbiome, as part of the coral holobiont (Ainsworth et al., 2017; Ricci et al., 2019; Pernice et al., 2020). Corals are currently seen as a coral holobiont, a complex biological community comprising the coral polyp host, zooxanthellae (algae *Symbiodinium* critical for coral photosymbiosis) and diverse tissue-, mucus- and skeleton-associated algae, bacteria, archaea and viruses (Rosenberg et al., 2007). The coral microbiomes, including skeleton microbiome, are crucial for coral health and reef survival (Fine and Loya, 2002; Rosenberg and Loya, 2013; Pernice et al., 2020). Skeleton microbiome (both boring microbes as well as cryptoendoliths which are microbes living in pores of the skeleton) of modern corals is recently commonly reported, but microborings are rarely documented in details (e.g., Lukas 1974; Le Campion-Alsumard et al., 1995; Nothdurft et al., 2007; Nothdurft and Webb, 2009).

The fossil record of microborings produced by symbiotic endoliths is very sparse, but they reported from Tabulata, Rugosa (Elias and Lee, 1993), Scleractinia and Octocorallia (Kołodziej et al., 2012, 2016; Salamon, 2017; Salamon et al., 2018). These rare examples provide insight into the poorly recognised skeleton microbiome of ancient corals. The modern examples show that microborers inhabiting the skeletons of living corals contribute to bioerosion, but also may be beneficial to corals. Euendolithic algae facilitate coral survival during bleaching events as an alternative source of photoassimilates (Fine and Loya, 2002; and for review:; Tribollet, 2008; Rosenberg and Loya, 2013). Endolithic fungi are potentially parasitic (e.g., Golubic et al., 2005), but they can also be positively involved in nitrogen metabolism of the coral holobiont (e.g., Wegley et al., 2007). Endolithic microbes *in vivo* associated with host organisms can be described as symbiotic endoliths (compare Gehman and Harely, 2019). Symbiotic associations involve relationships in which microbes have both positive (mutualistic) and negative (parasitic) effects on their host, which is in agreement with the original (19th century) meaning of the word 'symbiosis' (e.g., Peacock, 2011; Hussa and Goodrich-Blair, 2013).

Microborings *I. elegans* – commonly assumed to be a product of *O. quekettii* – are known since the Ordovician. Interestingly, most common microborings produced by coral-associated microendoliths in the corals studied here, in Palaeocene–Eocene (preliminary studies: Salamon, 2017; Salamon et al., 2019) and Jurassic

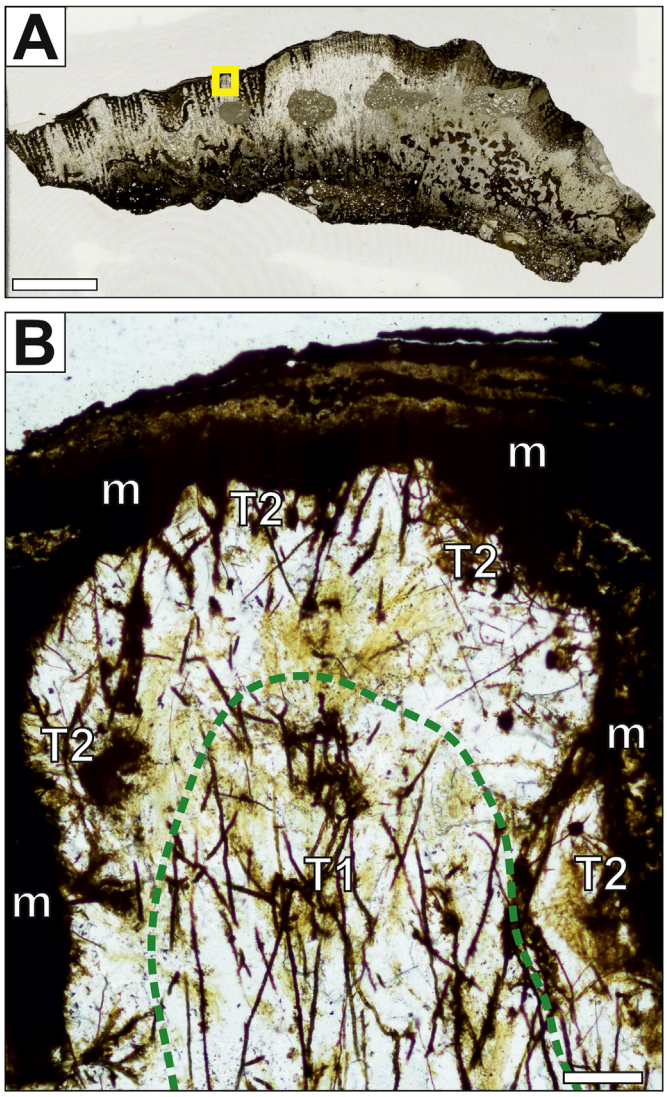

Fig. 6. The general variety and distribution of microborings in different parts of the coral radial element (septum) in a longitudinal section. **A.** Scan of the thin section showing the entire colony. **B.** Close-up of A under the petrographic microscope. Type 1 microborings inside the septa (T1) is outlined by dotted line. Type 2 microborings occur at the upper margin of the septum (outermost part of the colony; T2). The septum is surrounded by ferruginous crust (m). Scale bars = 5 mm for A; 100 μm for B.

corals (Salamon, unpublished observations) also represent *I. elegans.* These microborings (see also undermined microborings shown by Kołodziej et al., 2012, 2016) are oriented predominantly upward, like distribution of filaments of *O. quekettii* in modern live corals. It is possible that these traces could be produced by other green algae similar to *O. quekettii.* This species in the skeletons of scleractinian corals is not a single genotype, but at least seven different clades occur and are distributed along a depth gradient. It is possible that these clades may represent more than one species (Gutner-Hoch and Fine, 2011). We suggest that further studies should include the morphological variability of the microborings left by these algae in modern and fossil corals, which will improve our understanding of microborings classified as *I. elegans.*

Diagenesis is possibly the main reason for the sparse fossil record of microborings produced by symbiotic microendoliths. Coral skeletons are usually affected by the transformation of aragonite into calcite, recrystallisation or dissolution. Microborings filled with calcite-cement are difficult to recognise even in well-

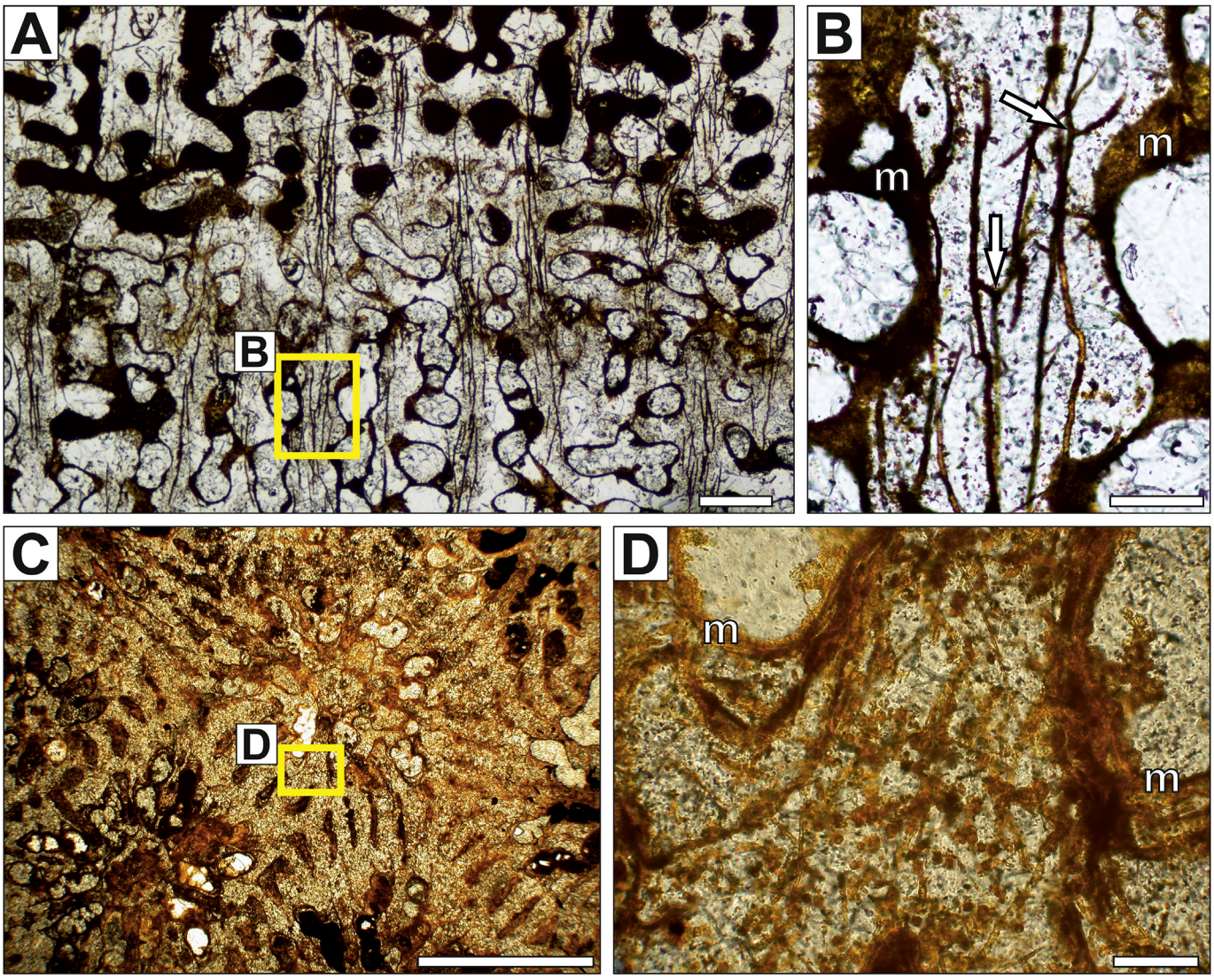

Fig. 7. Type 1 microborings in etched-thin sections under the petrographic microscope in longitudinal (A–B) and transverse sections (C–D). **A.** General view of the internal part of the colony. The straight galleries of *Ichnoreticulina elegans* are clearly visible in the skeleton. **B.** Close-up of A. The bifurcations (white arrows) indicate the upward boring direction. **C.** General view of corallites. **D.** Close-up of C. The upward-oriented tubular microborings in a transverse section are marked as numerous dotes. Thin ferruginous films (m) occur on the surface of septa (B, D). Scale bars = 200 μm for A; 50 μm for B; 1 mm for C; 100 μm for D.

preserved skeletons. Some larger (10–40 μm) calcite-filled microborings can be easily recognised under the petrographic microscope, but such reports are very rare (Kołodziej et al., 2012, 2016). Empty microborings can be expected in specimens that are poorly affected by diagenesis, and thus of Cenozoic rather than Mesozoic age. There are exceptions, however, such as the empty microborings in Upper Jurassic corals (but still aragonitic; Roniewicz, 1984) occurring in Quaternary glacial sediments (Salamon, unpublished observations).

Detailed ichnological studies require SEM studies of the resin casts of microborings, obtained using the epoxy vacuum cast-embedding technique. There are simple methods for rapid detection of empty microborings (Salamon et al., 2019), hence for the selection of samples for further SEM studies. In order to reveal the fossil skeleton microbiome, it is necessary to also study corals of older age, where microborings are rarely left empty. The study of corals with taphonomic traits like in the Cenomanian corals studied here (microborings filled with iron-rich or other non-carbonate minerals), which allow an examination of the natural casts of microborings even in recrystallized skeletons, are of particular significance. Studies of the fossil skeleton microbiome should include corals of different ages, and environmental and palaeogeographic settings. Such studies will hopefully expand the current minimal knowledge of the skeleton microbiome of fossil corals.

The presence of *in vivo* associated microendoliths is a rare phenomenon among modern organisms, and very sparse in fossils. They are known in modern stylasterid hydrozoans (Pica et al., 2016). Symbiotic endolithic cyanobacteria were reported from modern bivalves. Microbial endoliths take part in bioerosion of

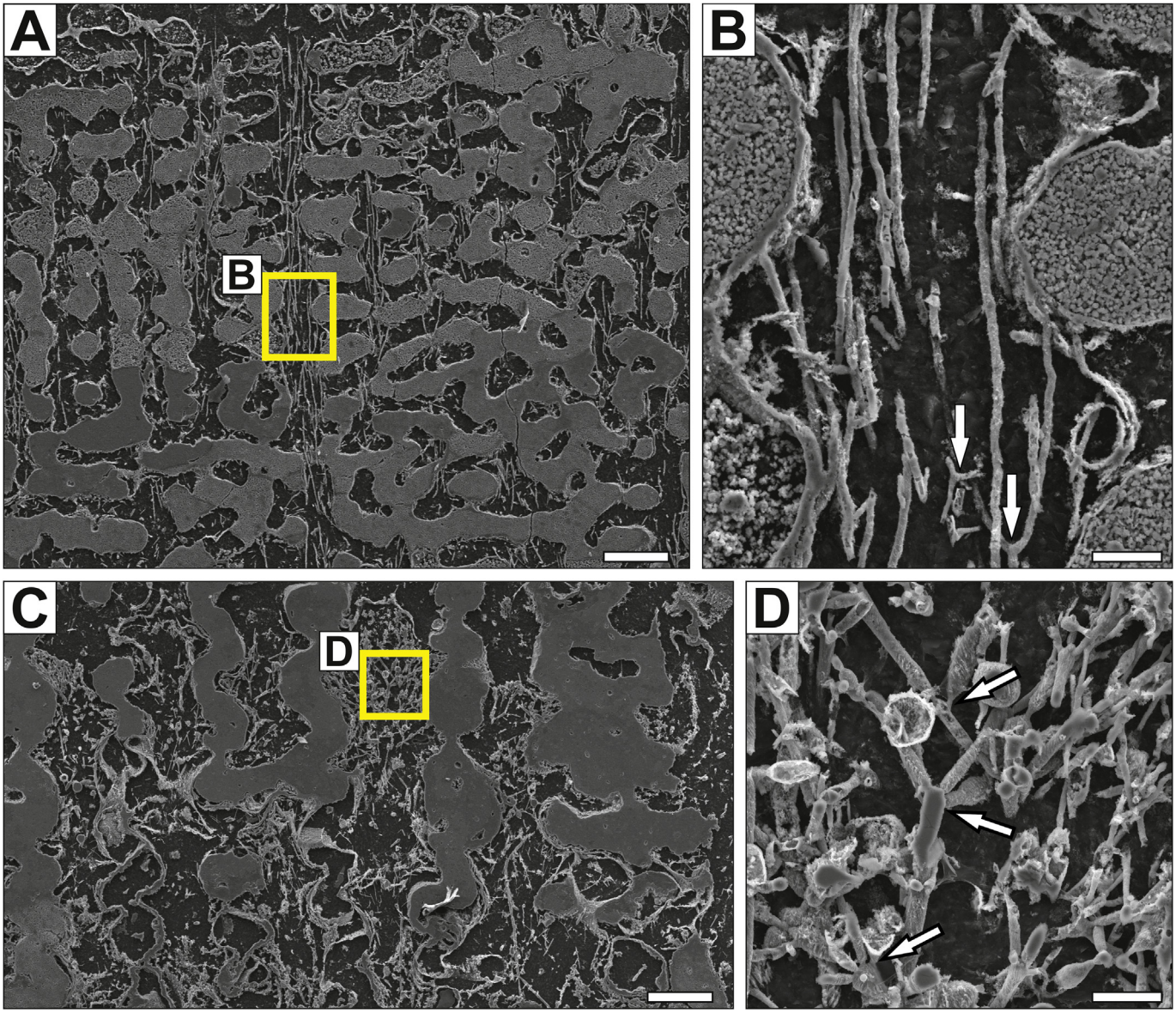

Fig. 8. Type 1 microborings in coral skeletons in the etched thin section under SEM in a longitudinal section. Interseptal space is completely filled with ferruginous deposit. **A.** General view. **B.** Close-up of A showing the upward-oriented galleries of *Ichnoreticulina elegans*. **C.** Dense networks of *Conchocelichnus seilacheri* located deep inside the colony. **D.** Close-up of C. Direction of bifurcations (arrows) of *I. elegans* (B) and *C. seilacheri* (D) indicates the upward orientation of both ichnospecies. Scale bars = 200 μm for A, C; 30 μm for B, C.

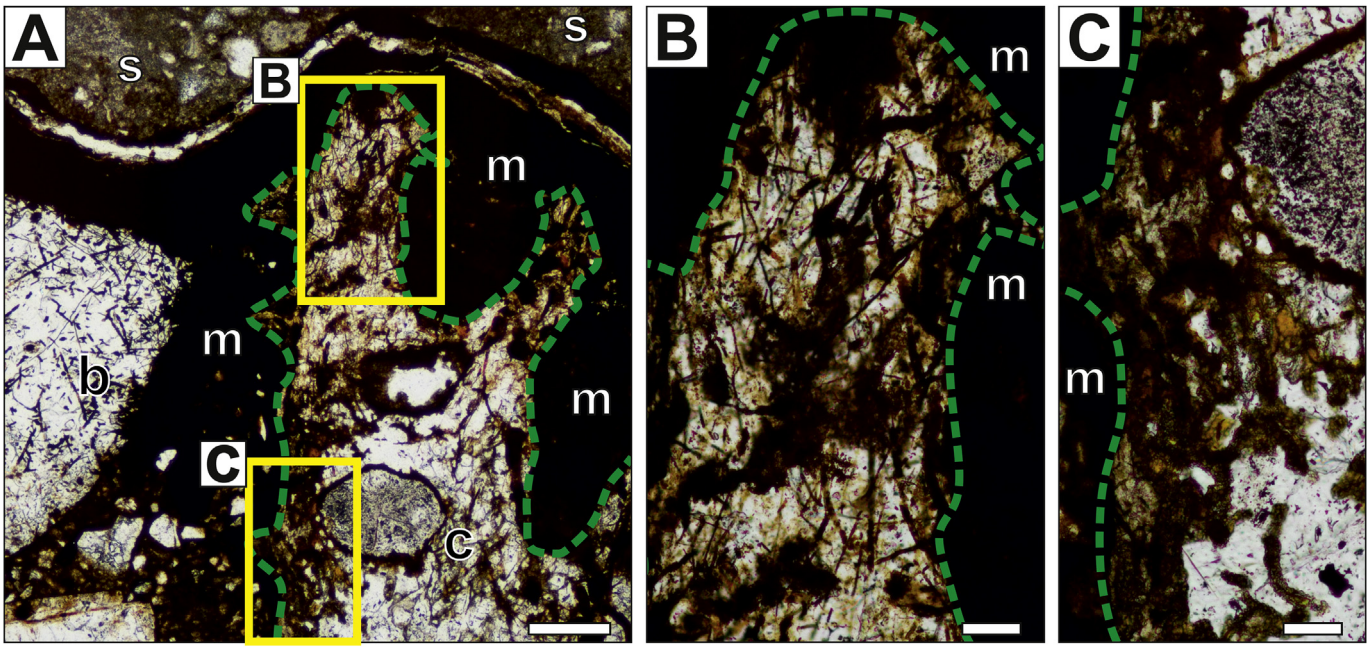

Fig. 9. Type 2 microborings in the thin section under the petrographic microscope in a longitudinal section. **A.** Numerous microborings in the coral septum (c) and a bioclast (b) trapped in a ferruginous crust (m); s – surrounding sediment. **B.** Network of undetermined thin microborings. **C.** Dense network of undetermined thicker, tubular microborings located close to the interseptal space. Scale bars = 200 μm for A; 50 μm for B, C.

bivalves (like in corals), weakening shell strength and leading to mechanical failure and death. However, these parasitic phototrophic endoliths can benefit their mussel hosts, and may be important mutualists during periods of intense heat stress due to the white discolouration caused by the activity of microendoliths (Zardi et al., 2016; Gehman and Harley, 2019). To the best of our knowledge, there are no fossil records of similar associations between bivalves (or other shell-bearing organisms) and microendoliths. It is certainly, like the skeleton microbiome of fossil corals, a topic worth of future investigation.

5.3. Type 2 microborings: traces produced post-mortem

Type 2 microborings were produced by microendoliths that penetrated skeletons from the surface down into the substrate. They are particularly common and clearly visible below some thick ferruginous crusts coating entire coral skeletons. It supports the interpretation that the ferruginous crusts are of microbial origin, even though microbial filaments are not observed in crusts (Gradziński et al., 1996), except those of microborings in clasts enclosed within crusts. Microendoliths attacked the denuded parts of dead corals (or dead parts of still living corals), and thus were produced post-mortem, as per the distribution pattern described by Le Campion-Alsumard et al. (1995). Most determined microborings were produced by chlorophyte alga *O. quekettii* (ichnospecies *I. elegans*), cyanobacteria *P. terebrans* (producer of *S. filosa*), and an unknown bacteria (producer of *S. serrata*).

Post-mortem microborings in biotic and abiotic substrates are common in both modern and fossil material. They provide information on bathymetry and other environmental conditions (Golubic et al., 1975; Vogel et al., 2000; Chazottes et al., 2009; Tribollet et al., 2011; Wisshak, 2012). Microborings *I. elegans* and *S. filosa* are common in the studied corals, but in many studies they were recognised in a wide range of geographical, bathymetrical, and environmental settings of modern seas (e.g., Radtke, 1991; Vogel et al., 2000; Wisshak et al., 2011) and are irrelevant to palaeoenvironmental conditions. Microborings described here occur on the surfaces of skeletal elements below microbialite crusts (upper colony surface), and below thin ferruginous films on skeletal elements. Interseptal space is a cryptic microenvironment characterised by lower light levels. *I. elegans* and *C. seilacheri* are produced by phototrophic microorganisms adapted to lower light levels (e.g., Halldal, 1968; Fork and Larkum, 1989; Shashar and Stambler, 1992; Koehne et al., 1999; Vogel et al., 2000; Radtke et al., 2016).

The small length of fragments in some galleries and the high density of some networks caused that some ichnospecies were hard to determine. However, general features of relatively thick microborings (ca 12 μm in diameter) suggest that they represent Fascichnus isp. produced by cyanobacteria *Hyella* sp. or *Irhopalia clavigera* (Golubic & Radtke, 2008) produced by chlorophyte Phaeophila dendroides (P. Crouan & H. Crouan) Batters, 1902 (compare Wisshak et al., 2011). These microendoliths are phototrophs occurring in the shallow euphotic zone, down to 60 m (Akpan and Farrow, 1984; Glaub, 1999; Wisshak et al., 2011) which is consistent with sedimentary and paleontological data of the studied material (Tröger, 1956). Further ichnotaxonomical studies of undetermined microborings are needed to provide more data on environmental factors.

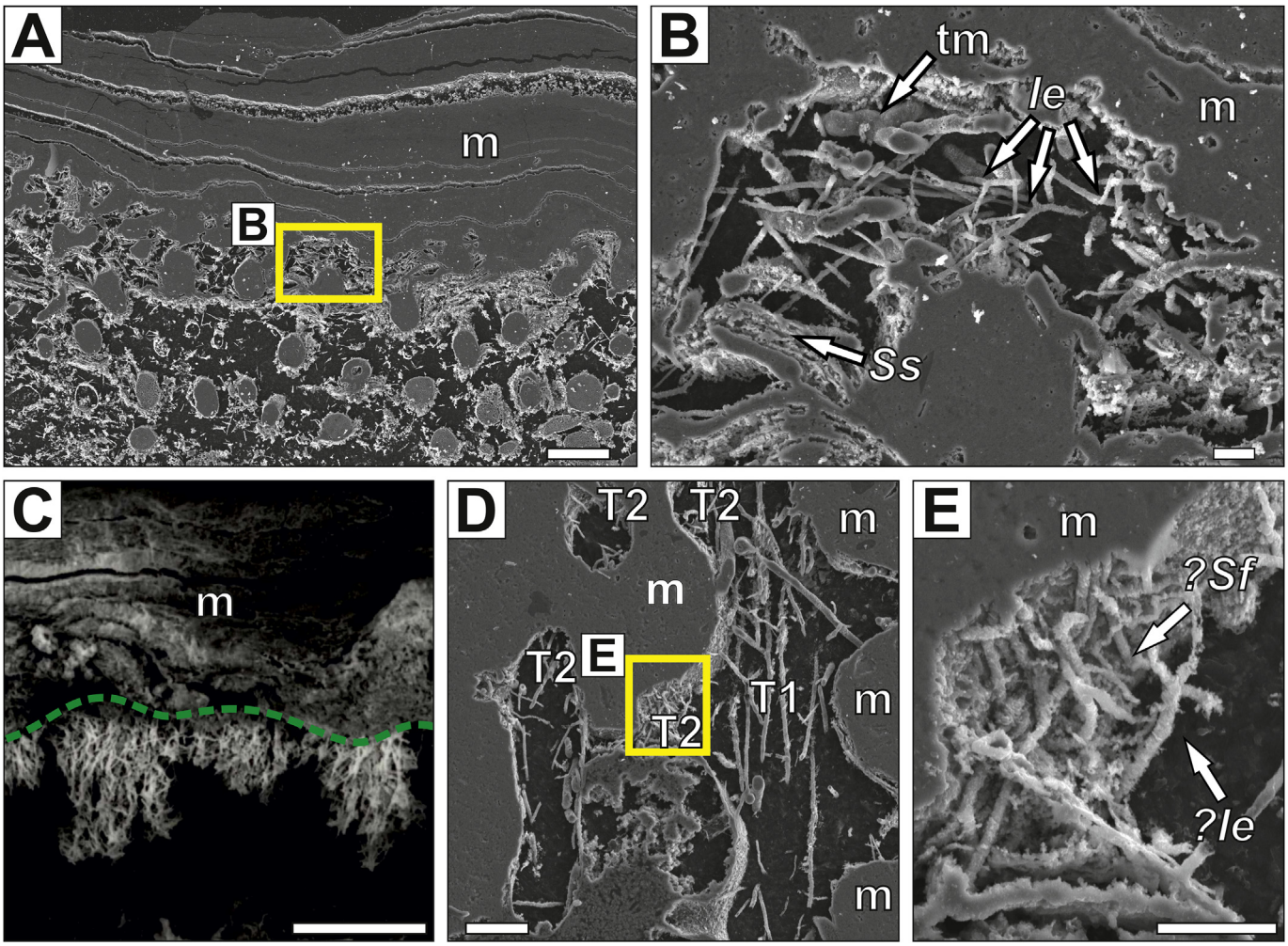

Fig. 10. Type 2 microborings in the etched thin sections under SEM in a longitudinal section. **A.** Dense network of various microborings at the marginal part of the colony below a ferruginous crust (m). **B.** Close-up of A. The network is dominated by undetermined thick microborings (tm), *Ichnoreticulina elegans* (*Ie*) and *Scolecia serrata* (*Ss*). **C.** Dense networks of ?*Scolecia filosa* and undetermined microborings oriented perpendicular to the outermost surface of the colony. **D.** Type 2 microborings (T2) below the surface of the septum in a longitudinal section (m – ferruginous crust in the interseptal space). Galleries of Type 1 microborings (T1) are clearly visible in the central part of the skeletal elements. **E.** Close-up of D. Randomly oriented galleries of ?*S. filosa* (?*Sf*) and ?*I. elegans* (?*Ie*). Scale bars = 200 μm for A, C; 20 μm for B, E; 50 μm for D.

6. Conclusions

1. The upper Cenomanian rocky-shore conglomerate (Dölzschen Formation) in the abandoned Ratssteinbruch quarry in Dresden (Saxony, Germany) contains a rich coral fauna. Entire coral specimens (colonies mostly up to 5 cm in diameter) are encrusted by ferruginous microbial crusts (mostly 1–2 mm in thickness), while septa and other skeletal elements are coated by very thin, micrometre-thick ferruginous films. Ubiquitous microborings (2–12 μm in diameter) occur both in the outer and the inner parts of coral colonies. Three-dimensional, natural, ferruginous casts of microboring tunnels (galleries) offer the potential for studies under petrographic and scanning electron microscopes. Studying the natural casts of microborings showed that two types of microborings can be distinguished in respect of the timing of their production in relation to coral life.
2. Type 1 microborings are typically distributed along the septa in the direction of the coral growth. The most common traces represent *Ichnoreticulina elegans* (commonly assumed to be produced by the chlorophyte green alga *Ostreobium quekettii*). Others belong to *Scolecia filosa* (producer: cyanobacteria *Plectonema terebrans*) and *Conchocelichnus seilacheri* (trace of red algae). Microborings were produced in living, growing corals by coral-associated microendoliths (*in vivo*). Type 1 microborings have palaeobiological inferences, providing insight into the very poorly recognised skeleton microbiome of fossil corals. Current studies indicate that, like in modern, living corals, the most common microendoliths in the Cenomanian corals were (based on microborings *I. elegans*) *O. quekettii* or other green algae close to this species. This ichnospecies is known since Ordovician, but described here examples are the oldest record of *I. elegans* in the microbiome of fossil corals.
3. Type 2 microborings were produced after coral death (post-mortem). They are very common below microbial ferruginous crusts coating the entire colony and below thin ferruginous films coating skeletal elements. Traces are represented by *I. elegans*, *Scolecia serrata* (producer: unknown bacteria), and *S. filosa.* The possible presence of *Fascichnus* isp (producer: cyanobacteria *Hyella* sp.). and *Irhopalia catenata* (producer: chlorophyte alga *Phaeophila dendroides*) suggests that the taphonomic processes affecting corals took place in a relatively shallow-water sedimentary environment, which is consistent with previous sedimentary and paleontological data.

4. Post-mortem, iron-filled microborings occur also below ferruginous microbial crusts on other larger fossils (bivalves, gastropods). Microborings are absent or rare in smaller fossils not having such encrustations implying that biota in the conglomerate derived from different parts of the shallow-water environment with contrasting taphonomic processes.

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